Temperature and masting control Norway spruce growth, but with high individual tree variability

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Highlights

- Cone production is synchronised between trees, but dominated by “super-producers”
- Cone and seed production show no long-term temporal trend despite strong regional warming
- Radial growth is lower in mast years that coincide with unfavourable climate (cool summer temperature)
- Growth reductions in mast years are restricted to “super-producers”

Abstract

Tree growth and reproduction are subject to trade-offs in resource allocation. At the same time, they are both influenced by climate. In this study, we combined long records of reproductive effort at the individual- (29 years), population- (41 years) and regional (up to 53 years) scale, and tree ring chronologies, to investigate the effects of climate and reproductive allocation on radial growth in an Alpine Norway spruce forest.

Seed and cone production was highly variable between years (mean individual CV = 1.39, population CV = 1.19), but showed high reproductive synchrony between individuals (mean inter-tree correlation = 0.72). No long-term trend in reproductive effort was detected over four decades of observations. At the stand scale, cone production was dominated by a small number of individuals ("super-producers"), who remained dominant over three decades.

Individual tree growth responded positively to summer temperature, but the response to cone production varied between individual trees. Consequently, we found some evidence that mast years were associated with a divergence in growth between high and low cone producing individuals, and a decline in within-population growth synchrony.

At the population level we found limited evidence of a relationship between growth and reproduction. Radial growth was lower than average in some mast years, but not in others. This was partly explained by summer temperature during the year of growth, with growth reductions restricted to mast years that coincided with colder than average summers. Regional mast records and tree ring chronologies provided some support to indicate that our results were consistent in other spruce stands, although the effect of mast years on growth appeared to vary between sites.

Tree ring variation at the individual and population level, and between-tree growth synchrony are influenced by masting, and consequently dendrochronologists should consider both the occurrence of masting and the individual differences in reproductive effort when interpreting tree ring datasets. Our results also indicate that tree ring chronologies contain information to facilitate reconstruction of mast events, which will help address outstanding questions regarding the future response of masting to climate change.

1. Introduction

Tree growth and reproduction are the endogenous processes that drive forest dynamics and tree population demography, along with mortality. Growth is strongly influenced by climate, through control on wood formation processes (Carrer *et al.*, 2017), and through complex effects on resource accumulation and availability (Hayat *et al.*, 2017; Medlyn *et al.*, 2002). Likewise, allocation to reproduction is also strongly influenced by climate, directly via climate cues (Vacchiano *et al.*, 2017) that trigger flowering and affect pollination efficiency (Koenig *et al.*, 2015), and indirectly through the regulation of available resources (Pearse, Koenig and Kelly, 2016; AllenMillard and Richardson, 2017). Growth and reproduction are themselves related through a trade-off for resources (Barringer, Koenig and Knops, 2013; Obeso, 2002), which may itself vary in strength with climate (Sletvold and Agren, 2015; Hacket-Pain, Lageard and Thomas, 2017; Villellas and Garcia, 2018). Consequently, integrating growth and reproduction data should allow a more complete understanding of the tree growth responses to climate, including climate extremes and long-term trends (Davi *et al.*, 2016; Hacket-Pain *et al.*, 2018; Lucas-Borja and Vacchiano, 2018).

Internal reserves in mature trees may be expected to buffer against the trade-off between growth and reproduction, but growth reductions in years of high reproductive investment are frequently reported (Barringer, Koenig and Knops, 2013; Hacket-Pain, Lageard and Thomas, 2017; Monks and Kelly, 2006; Selas *et al.*, 2002). Masting species may show particularly strong trade-offs as their reproductive strategy is characterised by highly variable allocation to reproduction (Kelly and Sork, 2002; Mencuccini, Piussi and Sulli, 1995; Pearse, Koenig and Kelly, 2016). Growth reductions in mast years have been reported in studies focused on Norway spruce, a typical masting tree species (Mencuccini and Piussi, 1995; Selas *et al.*, 2002), but other studies have failed to find evidence to support the existence of a trade-off between growth and reproduction in this species (Seifert and Mueller-Starck, 2009). There are various possible explanations for the conflicting reports of this

trade-off, including challenges in effectively measuring the cost of reproduction (Obeso, 2002), costs being offset by the use of reserves (Mund *et al.*, 2010) or compensatory carbon gain via photosynthesis in the tissues of the developing reproductive organs (Hoch, 2005). Alternatively, allocation to reproduction and growth may be positively correlated with the same climatic variables, so that growth and reproduction may be positively rather than negatively correlated (Despland and Houle, 1997). Additionally, under favourable growing conditions, a reduction in growth associated with investment in reproduction may be weaker or absent; i.e. the strength of the growth-reproduction trade-off may depend on stress or resource availability (Barringer, Koenig and Knops, 2013; Berdanier and Clark, 2016; Hacket-Pain, Lageard and Thomas, 2017). In these scenarios, a high investment in reproduction may not translate to a decrease in growth.

Additionally, allocation to reproduction is known to vary between individuals due to canopy position and microenvironmental conditions (Davi *et al.*, 2016; Greene *et al.*, 2002; Brooke *et al.*, 2019), tree age and size (Thomas, 2011; Krouchi, Derridj and Lefevre, 2004), genetic control (Seifert and Mueller-Starck, 2009), or other factors (note that these may not be independent). Consequently, cone production at the stand scale may be dominated by a subset of "super-producers" (Minor and Kobe, 2017; Brooke *et al.*, 2019). Such intraspecific variation in allocation to reproduction may result in variation in the cost of reproduction between individuals during population-wide mast years, so that any growth reductions may be greater in individuals that invest more heavily in reproduction (Patterson and Knapp, 2018). This would be consistent with numerous studies reporting lower growth in female individuals in dioecious species (Obeso, 2002). Furthermore, the cost of reproduction may vary at the individual scale due to differences in stored reserves or access to belowground resources. Individualistic growth responses to climate have previously been investigated using tree rings (Carrer, 2011; Buras *et al.*, 2018), but the potential for these to be driven by individualistic responses to reproduction remains underexplored.

To investigate how relationships between reproduction, growth and climate vary between individuals, and their interplay at the tree level, we used data from a Norway spruce population in the Italian Alps. Population-level data on reproduction was collected for the period 1971-2012, and 13 individual trees were monitored annually for cone production for 29 years (1983-2012, with no data from 2007). Tree ring samples were collected from these 13 individuals in 2013. We also use a network of spruce chronologies from the Alps and regional masting records from the MASTREE database (Ascoli *et al.*, 2017a) to test whether our results can be generalised for Alpine spruce forests.

We test the following hypotheses:

1. Seed production is synchronous at the population level, but cone production is dominated by "super-producers"

2. Years of high seed production are associated with reduced growth. The trade-off is stronger under unfavourable climatic conditions, in this case cool summers

3. Growth-reproduction trade-offs are stronger in "super-producers", resulting in reduced growth synchronisation in mast years, and growth divergence between "super-producers" and other trees

157 # 2. Methods

158

159 **2.1 Data collection**

160 Analysis focused on Norway spruce (*Picea abies* (L.) Karst.) forests located in the upper Travignolo
161 Valley (Trento, Italy) at 46.18° N, 11.45° E, between 1500 and 1900 m a.s.l (Paneveggio). The climate
162 is continental, with mean annual precipitation of 1250-1660 mm·year^{-1} and mean annual
163 temperature of 2.7°C. Spruce seed production has been monitored in Paneveggio since 1962 using
164 seed traps, although data collected prior to 1971 is considered potentially unreliable and was not
165 included in our analysis (Mencuccini, Piussi and Sulli, 1995). Seed traps were deployed in October,
166 and seeds were collected after snowmelt. Following collection, seeds were sorted and tested in
167 germination chambers. Counts of viable, predated and damaged seeds were used to quantify annual
168 reproductive effort.

169

170 In the same forest, long-term monitoring of annual reproductive effort by 13 individual trees was
171 conducted 1983-2012. All monitored individuals were located within 70 m from one another, and
172 individual tree reproduction was quantified by an annual cone count during June. Trees were located
173 at the edge of a gap created in the lower part of the forest (1520 m a.s.l.) for experimental forest
174 management purposes (Piussi, 1988). The stand was uneven aged, but represented by a single
175 canopy structure, with small differences in tree height. Cones were counted each year from the
176 same observation point, providing a consistent indicator of individual and aggregated cone
177 production. Except for 2007, cones were counted annually until 2013, when some trees were
178 windthrown (although only data to 2012 was used this analysis, to match the tree ring data – see
179 below). To extend the stand-level record of reproduction based on the average of the 13 individual
180 trees, a linear regression between annual mean seed count (across seed traps) and mean cone count
181 (across trees) for twelve years of overlap (1983-1994, $R^2 = 0.82$, $p<0.001$, Supp. Figure 1) was used to

create a 42-year record of population-level reproduction at this site (Figure 1, “cone index”), which consisted of predicted cone counts for the period 1971-1982 and observed cone counts 1983-2012.

In 2013, increment cores were extracted from the 13 individual trees that had been monitored for cone production, by taking two cores per tree at breast height (1.3 m). Cores were mounted and sanded with progressively finer sandpaper until tree ring boundaries were clearly visible. Tree ring widths were measured using a binocular microscope and LINTAB measuring devices (Rinntech, Heidelberg, Germany) to the nearest 0.01 mm. The accuracy of visual cross-dating and measurements was checked with the COFECHA program (Grissino-Mayer, 2001). Cross-dated series belonging to the same tree were then averaged. Ring width series were detrended using a double-detrending protocol, first using a modified negative exponential curve to remove the age- or size-related trend, and then using a 20-year cubic spline with frequency cut-off of 0.5 to remove trends associated with disturbance and canopy dynamics (Cook and Peters, 1981). The individual tree ring series were pre-whitened to reduce temporal autocorrelation by fitting an autoregressive model, whose optimal order was selected to minimise the Akaike’s Information Criterion (AIC) score. A stand ring width index (RWI) chronology was created by averaging the detrended series from the 13 trees. Basal area increment (BAI) was calculated for individual trees using the formula:

$$BAI_t = \pi(r_t^2 - r_{t-1}^2)$$, where r is the radius of the tree in year t.

Processing of ring width measurements was conducted using the dplR package in R (Bunn, 2008; R Development Core Team, 2016). Monthly climate data for Paneveggio was extracted from the HISTALP dataset at 5’x5’ resolution (Auer *et al.*, 2007), using the histalp package (Zang, 2018).

208 **2.2 Individual and population-scale analysis**

209 Trends and patterns of seed and cone production were assessed for Paneveggio using population
210 and individual-tree data (Vacchiano *et al.*, 2018). Synchrony of reproductive effort between
211 individuals was quantified as the mean Pearson product-moment correlation between pairs of
212 individual trees, and variability was assessed using the coefficient of variation (CV). Autocorrelation
213 functions (ACF) were used to test for serial correlation in seed and cone production time-series. We
214 identified mast events when reproductive effort exceed one standard deviation from the long-term
215 mean (LaMontagne and Boutin, 2009). We hypothesised that "super-producers" would dominate
216 overall cone production at the stand scale, either due to larger cone crops in mast years, or more
217 frequent large cone crops (or both). To test this, we defined individual-level "bumper crops" (the
218 individual-tree equivalent of a "mast year") as years when individual tree cone count exceed one
219 standard deviation from the mean cone count from all 13 individuals over whole the study period.
220
221 Relationships between reproduction and growth, and climate and growth were assessed using
222 generalised additive models (GAMs). Where GAMs indicated a linear relationship between two
223 variables (estimated degrees of freedom close to 1), we re-fitted using linear regression models. As
224 tree ring data (RWI) was detrended, we also removed long-term trends in the climate data using
225 linear regression. As cone production varied strongly between individuals, analysis was conducted at
226 the individual level, as well as the population-level. Effects of variable reproduction (between years)
227 on between-tree growth synchrony was tested by calculating inter-individual growth variability for
228 each year (using the CV). A higher CV for an individual year indicated greater between-tree growth
229 variability, representing lower growth synchrony. To test for growth divergence between heavy and
230 light cone producers, we created a mean RWI chronology of heavy cone producers, and compared
231 this to a mean RWI chronology of the other trees. We defined heavy cone producers as individual
232 trees with above average cone counts across the whole study period.
233

234 **2.3 Regional datasets and analysis**

235 To test the generality of our results from Paneveggio, we analysed other spruce tree ring
236 chronologies from the Alpine region (Italian and Swiss Alps) together with regional records of spruce
237 mast years. Tree ring chronologies from the International Tree Ring Data Bank (ITRDB) (**insert**
238 **reference for the chronologies SWIT332, 279, 256 and 329 – we cannot do this at the moment at**
239 **the ITRDB is unavailable during the US Government shutdown – this will need to be added later)**
240 were combined with existing and new tree-ring chronologies from the Italian Alps (Table 2).
241 Detrending and chronology building followed the protocol used for the Paneveggio site. Regional
242 masting chronologies were developed for Switzerland (NUTS-1 region CH0), Slovenia (SI0) and
243 Northwest Italy (ITC) using the MASTREE database (Ascoli *et al.*, 2017a). In this dataset, annual seed
244 production is summarised in the database using five ordinal classes. Where multiple records existed
245 in a given year for the same NUTS-1 region, the modal value was used, following the method of
246 Vacchiano *et al*. (2017). In this regional-scale analysis, and due to a limited sample size (number of
247 years), ordinal data was then reclassified to a binary scale, comprising mast years (category 4 and 5)
248 and non-mast years (category 1-3) (Ascoli *et al.*, 2017b). The cruts package (Taylor and Parida, 2016)
249 was used to create NUTS-1 regional climate series from the CRU TS 3.23 gridded dataset (Harris *et*
250 *al.*, 2014), as region-wide means of individual-cell monthly values.
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3. Results

3.1 Seed production: variability between years and individuals

Cone production was highly variable at Paneveggio, both between individuals and between years. Individual tree coefficient of variation (CV_i) for cone counts across the period 1983-2012 varied between 1.11 and 1.97 (mean = 1.39), and the CV of the mean population cone count chronology (population-level CV, CV_p) was 1.19 (1983-2012). The CV_p for seed trap data 1971-2012 was 1.28. Cone production and seed counts had significant negative autocorrelation at lag -1 year (Supp. Figure 2). The extended 1971-2012 cone index, developed using a combination of seed trap data and mean cone counts, indicated the presence of large mast years in 1976, 1981 and 1995 (cone index >2 standard deviations from the mean), with additional mast years (>1 SD) in 1985 and 1988. The overall distribution of seed production during the period 1971-2012 was a continuous reserve J-shaped distribution (Figure 1D and Supp. Figure 3). A Hartigans' dip-test indicated no evidence of multimodality ($p>>0.05$ for seed count, cone count and combined cone index). In 1997 and 2008 no cones were counted on any of the 13 individuals, but in every other year cones were observed on at least one individual. The seed-trap datasets recorded some seed fall in every year – i.e. there were no years with zero recorded spruce seed production. The full 1971-2012 cone index chronology showed no long-term linear trend (regression of seed production versus year, $p > 0.05$), and this was also the case individually for the seed-trap dataset (1971-1994) and the mean cone-count dataset (1983-2012) (Supp. Figure 4). For the individual tree cone-count series (1983-2012), linear trends through time were also insignificant for all trees (Supp. Figure 4).

Cone production varied strongly between the 13 individual trees, and most cones were produced by a small proportion of individuals (Figure 1). The highest producing individual (ID_01) produced 26.3% of all produced cones (1983-2012), x2.5 the next highest producer. The lowest producer was responsible for only 1.7% of total cones. Bumper cone crops associated with individual trees were

generally quite rare (Figure 1A). Most tree produced between one and four such bumper crops over the 29 years of observation, while two individuals failed to produce a single bumper crops. In contrast, one individual (ID_01) produced 13 individual bumper crops, equivalent to almost one every two years on average. Total cone production (1983-2012) was correlated with tree diameter ($r= 0.539$, $p=0.057$, Supp. Figure 5), and there was a significant positive correlation with Basal Area Increment (BAI) 1983-2012 (Supp. Figure 6). However, with only thirteen trees these relationships were difficult to quantify, and both relationships were dependent on the inclusion of the highest producing individual (ID_01). Correlations were insignificant between total cone production (1983-2012) and tree age (estimated by counting the total number of measured tree rings).

Heavy cone producers remained heavy producers over at least three decades (Figure 1). For example, excluding the two years when no individuals produced any cones, the highest producing tree (ID_01) was the top-ranked producer 19 times (19/28 = 67.9%, highest producer in 2/3 of individual years), and the five individuals with the highest mean rank took 67% of the available annual top five ranking positions over 28 years. With 13 individual trees, an individual could expect to be in the top five 38% of all years if ranking was random. In contrast, the lowest ranking tree (ID_10) was in the top five on only three occasions, and the five lowest ranking individuals took only 25% of the available top five positions.

While highly variable between years and between individuals, cone production was synchronised between trees (Figure 1). Mean inter-tree correlation was 0.72 (min=0.33, max=0.91, median = 0.73). Cone and seed production at Paneveggio was also strongly synchronised with other Alpine masting chronologies for spruce. For example, high cone or seed counts were reported from spruce in 1995 in many of the records contained in the MASTREE database (Ascoli et al. 2017b). Cone index was positively correlated with neighbouring regional masting chronologies developed for cone and seed counts for CH0 (Switzerland) ($rho= 0.71$, $p<0.001$, $n=30$), ITC (NW Italy) ($rh=0.44$, $p=0.129$, $n=12$) and SI0 (Slovenia) ($rh=0.13$, $p=0.049$, $n=30$).

Table 1. Site and chronologies statistics for all sites. All statistics are reported for residual prewhitened chronology. EPS = Expressed Population Signal, rbar = inter-series correlation, SNR = signal-to-noise ratio, AC_1 = first order autocorrelation, MS = mean sensitivity

Site	Lat	Lon	Elev	Period*	Length*	N° trees	EPS	rbar	SNR	Mean (RWI)	SD (RWI)	AC_1 (RWI)	MS
PAN	46.18	11.45	1520	1813-2012	200	13	0.893	0.446	8.34	0.988	0.121	-0.072	0.122
PAN (study period)	46.18	11.45	1520	1971-2012	42	13	0.910	0.436	10.06	0.998	0.075	-0.065	0.085
SWIT332	46.46	9.18	1660	1842-2005	164	10	0.930	0.449	13.34	0.998	0.098	0.050	0.110
SWIT279	46.59	7.98	1850	1689-2011	323	25	0.924	0.455	12.21	0.988	0.121	0.023	0.131
SWIT256	46.30	7.72	900	1882-2005	124	12	0.941	0.527	15.892	0.989	0.218	-0.001	0.260
SWIT329	46.27	7.03	1440	1907-2005	99	16	0.948	0.405	18.239	0.998	0.114	-0.191	0.146
BREP	46.19	10.85	1550	1851-2010	160	20	0.903	0.353	9.341	0.994	0.090	-0.074	0.100
MASP	46.27	9.58	1150	1897-2013	117	31	0.927	0.375	12.693	0.999	0.113	-0.037	0.132
SALP	45.05	6.90	1800	1806-2017	212	25	0.823	0.284	4.649	0.997	0.112	-0.081	0.120
VENP	46.66	10.52	1500	1880-2017	138	10	0.873	0.460	6.868	0.990	0.145	-0.076	0.177
VIEP	45.64	7.27	1500	1842-2016	175	12	0.882	0.405	7.468	0.992	0.100	-0.136	0.117

* Note that period and length are taken from the residual prewhitened chronology, and therefore do not represent the full period of the raw chronology.

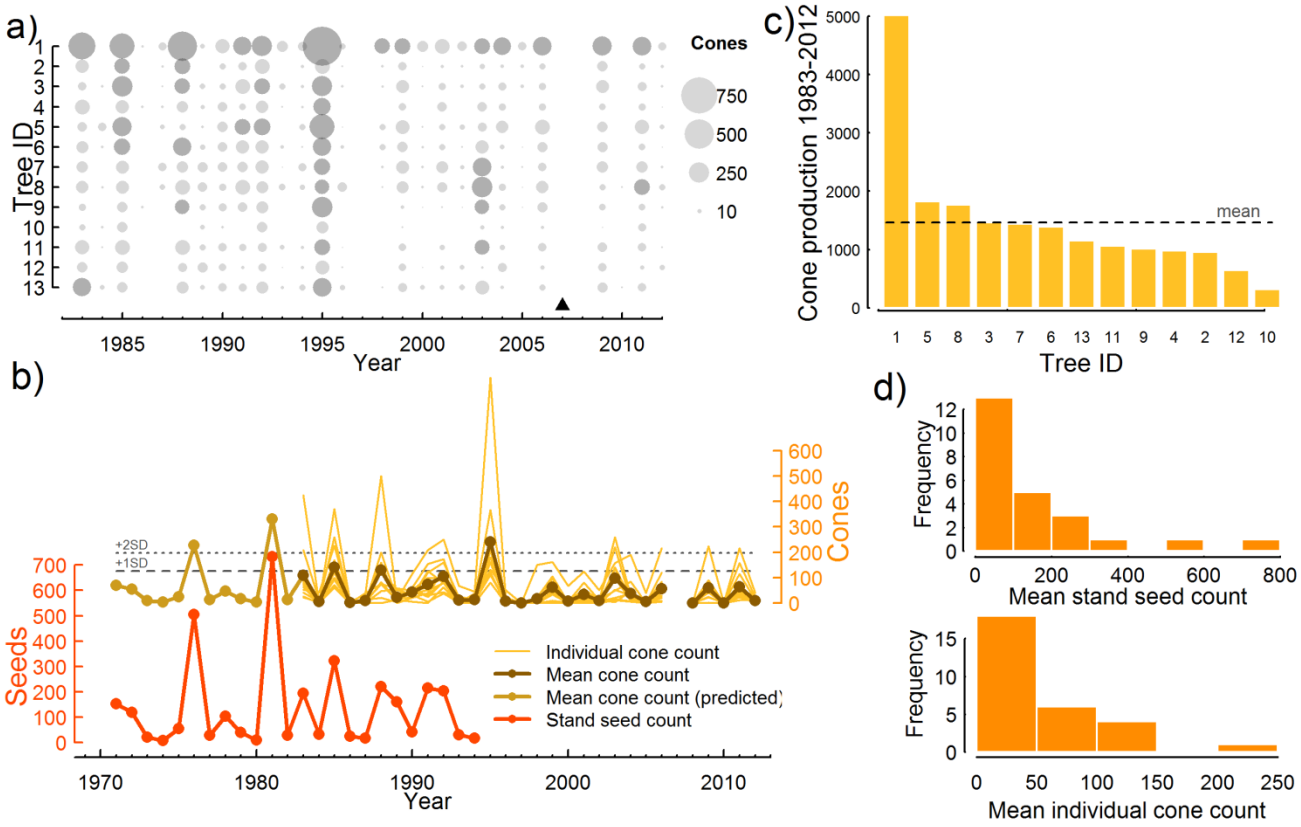


Figure 1. Cone and seed production at Paneveggio a) Individual tree cone counts 1983-2012. Symbol size is proportional to individual cone count, and shading indicates a bumper cone crop (individual cone production greater than the mean of all trees across the study period). Triangle indicates year with no data (2007). b) Individual tree cone counts (yellow) and the stand mean (dark brown) for the period 1983-2012, and predicted stand mean cone count for the period 1971-1982 (light brown). Dashed and dotted lines indicate +1 and +2 standard deviations from the mean, the definitions of mast and large mast year respectively. Stand-level seed counts (orange, 1971-1994). Observed and predicted cone counts are combined for the period 1971-2012 ("Cone index"), and are used in the rest of the analysis. c) Total cone production over the study period for the 13 monitored trees. The dashed line indicates the mean cone production. d) Frequency plots for stand-level seed count (1971-1994) and mean individual cone count (1983-2012).

3.2 Stand-scale growth-reproduction trade-offs

The relationship between stand-level ring width index (RWI) (mean of the 13 trees) and the combined stand cone index was weak and insignificant (r = -0.128, p = 0.424). This was consistent when analysed using the seed-count data only (1971-1994, r = -0.127, p = 0.555), and the cone count data only (1982-2012, r = -0.081, p = 0.676). Relationships were also insignificant when tested using GAMs (i.e. allowing for non-linear

relationships, results not shown). Some mast years were associated with low growth (e.g. 1981, 1995), but the large mast year in 1976 was associated with above average growth (Figure 2). Summer temperature (mean of May-July) was positively correlated with RWI for the period 1971-2012, ($r = 0.313$, $p = 0.044$; see also Figure 3D), and appeared to influence the response of RWI to cone index. In warm summers (summer temperature > 1971-2012 mean), there was no significant response to reproduction ($r = 0.169$, $p = 0.48$), but in cool summers cone index and RWI were negatively- correlated ($r = -0.471$, $p = 0.031$) (Figure 2). This indicated that a growth-reproduction trade-off was restricted to cool summers, where cone index explained 22% of variation in RWI (but <2% in analysis including all years, Figure 2B). However, with only five mast years in the 42-year record, and as the significant relationship in cool summers is dependent on the inclusion of the two large mast years in 1981 and 1995, this result should be treated with caution.

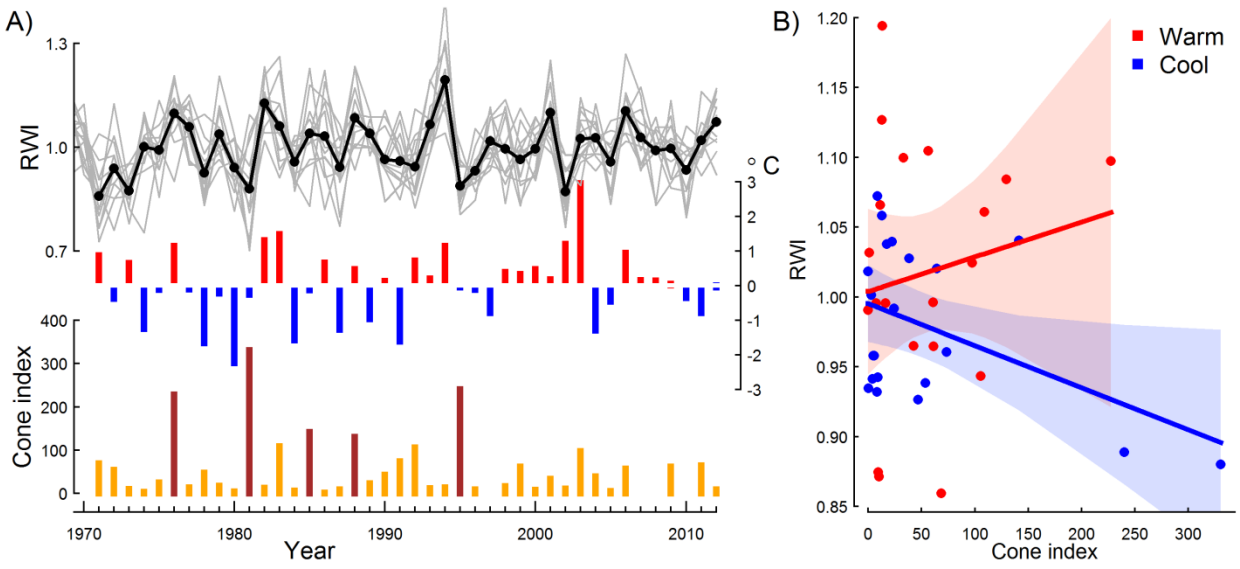


Figure 2. A) Time series with individual and mean stand RWI chronologies, May-July temperature anomalies and cone index. For temperature, red and blue bars indicate positive and negative temperature anomalies respectively. Mast years (cone index greater than one standard deviation from the mean) are plotted in dark brown. Note that the temperature anomalies are for detrended summer temperature (i.e. the linear trend in temperature is removed). B) The linear regressions for RWI ~ cone index for cold (blue) and warm (red) summers (1971-2012), including 95% confidence intervals.

To test the generality of these results, growth responses to regional mast years (MASTREE database) were tested for a network of Alpine spruce chronologies. Some sites showed lower growth in regional mast years, particularly those in northwest Italy (ITC: MASP, SALP and VIEP), and also the Swiss site SWIT256, but the growth reduction in mast years were small and marginally significant for only one site (VIEP, $p=0.048$) (Supp. Figure 7). The lack of a strong and significant relationship between RWI and masting was therefore consistent with the results from Paneveggio. Short overlapping time series made it difficult to test whether growth reductions were stronger in colder summers, as found at Paneveggio (Supp. Figure 8).

3.3 Individualistic growth responses to climate and reproduction

The climate response of individuals showed some variation, but warmer summers were associated with high growth (Figure 3D). However, the growth response of individuals to reproduction showed more variation, both when tested against the corresponding individual tree cone counts (1983-2012, Figure 3B), and when tested against the stand-scale cone index (1971-2012, Figure 3C). However, the relationship was significant in only one individual (note that this was an individual with above-average cone production, but not ID_01, the outstanding super-producer). High investment in cone production (at an individual- and stand-level) was associated with lower growth in the individuals with higher cone productivity (Figure 3). Responses of growth to mast years were close to zero or even positive in individuals with low cone productivity (albeit non-significant). For example, in heavier cone producers, the growth reductions in the heaviest stand-scale mast years were approximately equivalent in magnitude to those associated with coolest summers (Figure 3C and 3D). In contrast, the lightest cone producers showed positive growth responses in these years, equivalent in magnitude to the growth increase associated with a warm summer (Figure 3C and 3D).

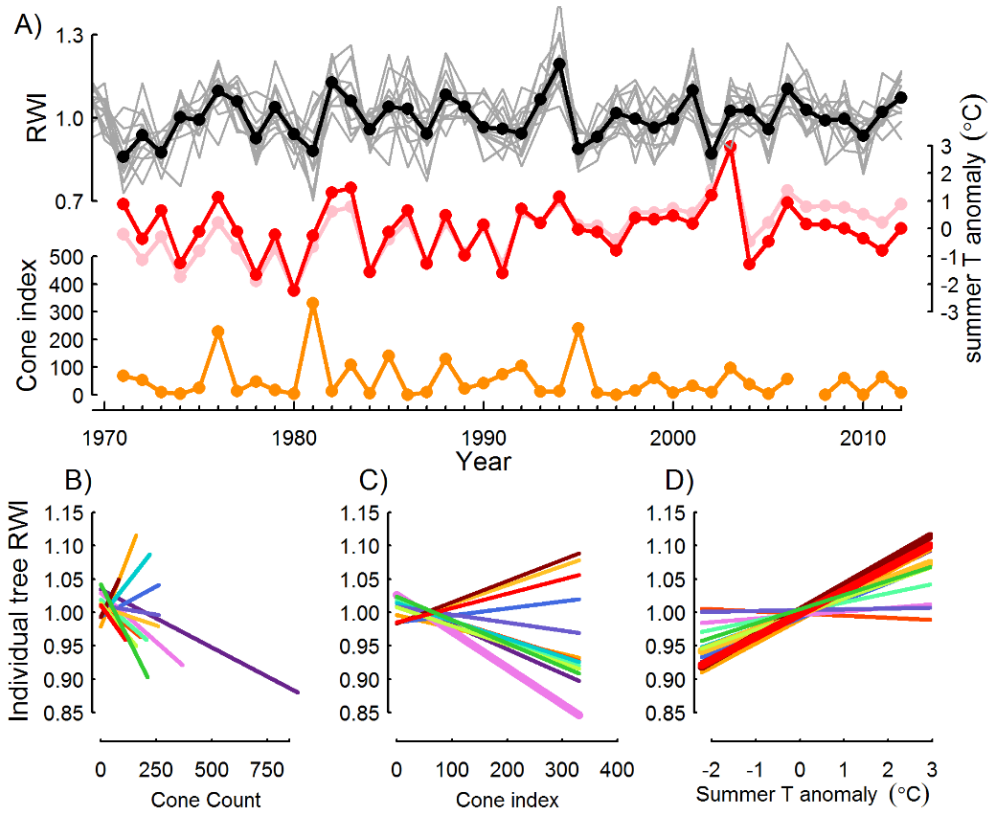
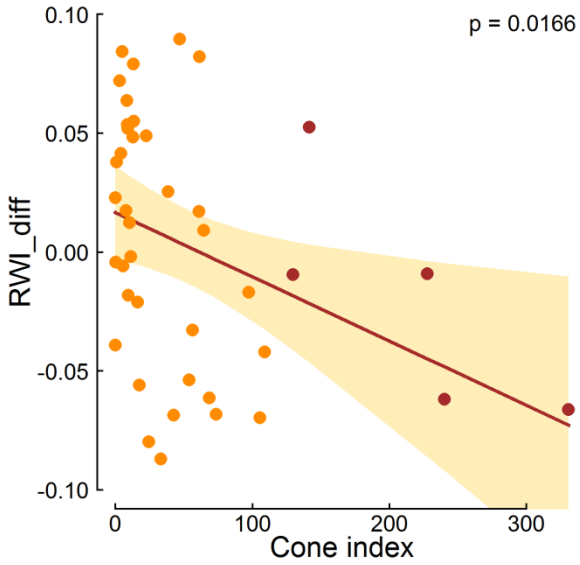


Figure 3. A) Time series with individual (thin lines) and stand-level (thick lines) RWI chronologies, summer temperature and cone index. The pink line represents raw summer temperature data, while the red line is linearly detrended data. The detrended data is used for the regression analysis. For B-D, only the regression lines are plotted. Each line represents the regression between individual tree RWI and B) corresponding individual tree cone counts (1982-2012), C) stand-scale cone index (1971-2012) D) summer temperature (detrended anomaly, 1971-2012). Thick lines indicate significant models. Line colour represents the individual tree ranking for total 1983-2012 cone count; heavy cone producers are purple/blue, and light producers are orange/red.

Overall, between-tree growth synchrony was high (rbar = 0.44, Table 1, and see also Figure 3A), representing a strong coherence in growth between years. However there were differences in synchrony between years; in other words, in some years individuals had very similar growth while in other years growth diverged between individuals (Figure 3A). The year with the highest stand-scale reproductive effort corresponded to the year with the highest between-individual growth CV (lowest growth synchrony) (1981, see Supp. Figure 9). There was a significant relationship between cone index and growth CV (Supp. Figure 9), suggesting that

high reproductive effort (at the stand scale) was associated with a decline in growth synchrony between individuals. However, the significance of the relationship was dependent on the inclusion of 1981, the year with highest cone index and between-tree growth CV. Without 1981, the relationship between-tree growth CV and cone index became insignificant. A similarly mixed picture emerged from analysis of between-individual growth CV for other regional chronologies (Supp. Figure 10). Between-tree growth synchrony decreased in mast years at some sites (e.g. VIEP, SWIT279) although this was never statistically significant and sample size was always low.

We also compared the RWI of heavy producers and other trees, to test whether mast years were associated with a growth divergence ($RWI_{diff} = RWI_{heavy} - RWI_{light}$). Heavy producers were defined as individuals with greater than average cone production 1983-2012 (Figure 1c). Overall the correlation between RWI timeseries of heavy and other trees was high ($r=0.81$, $p<0.001$) However, RWI_{diff} varied according to stand cone index. The relationship between RWI_{diff} and cone index appeared to be asymmetric, but in mast years heavy producers had lower growth relative to light producers (Figure 4). The difference was largest in the heaviest mast years (Figure 4). The relationship was even stronger if RWI_{light} was calculated for the equivalent three lightest producers, rather than for all other trees (results not shown).



402

403 **Figure 4.** Relationship between RWI_{diff} and stand-level cone index (1971-2012), with a 95% confidence interval.

404 Negative values indicate that heavy producing trees had lower growth than other trees. Brown points represent mast

405 years at the stand scale.

406

407

4. Discussion

4.1 Characteristics of cone production

Cone production at Paneveggio showed characteristics associated with masting. The stand-level CV_p for cone production was almost identical to that reported by Selas *et al.* (2002) for Norway spruce in Norway (1.20), and consistent with other reported values for spruce species and other masting species (Herrera *et al.*, 1998; Koenig and Knops, 2000; Lamontagne and Boutin, 2007). In the heaviest mast years, cone index at the stand scale was six times greater than the long-term mean, representing a substantial resource investment. At the individual tree scale the contrast was even more extreme. In 1995 tree ID_01 produced 18 times more cones that the mean cone production of all trees 1982-2012, and this individual was responsible for 26% of all the cones produced over the study period (by 13 individuals). Various factors may explain such individual variability in reproductive output, including tree age, size, microenvironmental conditions, resource availability, and genetics (Davi *et al.*, 2016; Greene *et al.*, 2002; Seifert and Mueller-Starck, 2009; Thomas, 2011; Brooke *et al.*, 2019), although with individual-tree data for only 13 trees, it was not possible to identify the factors controlling long-term cone productivity, or robustly test scaling with tree size. However, our data hinted that high cone production was associated with larger, faster growing trees. Notably, heavy cone producers retained their ranking over three decades. For example, the highest overall cone producer (ID_01) was the heaviest individual producer in two thirds of all years, consistent with the definition of "super-producer" suggested by Minor and Kobe (2017). Previous studies have also indicated that the relative reproductive performance of individual trees can be maintained over multiple years, but have relied on shorter datasets where long-term trends are difficult to identify (Healy, Lewis and Boose, 1999; Krouchi, Derridj and Lefevre, 2004; Linhart and Mitton, 1985).

While variable between years, reproduction was remarkably synchronised between trees (r=0.72), with all trees located within 70 m from one another. Synchrony of seed production declines with distance (Koenig and Knops, 2000), although not significantly at local scales (Lamontagne and Boutin, 2007). However, the

observed between-tree synchrony in cone counts was higher than that reported by LaMontagne and Boutin (2007) for *Picea glauca*, and represents a highly synchronised variation in resource allocation at the stand scale. Previous studies indicate that this synchronisation is also strong between Alpine spruce stands at local scales (MencucciniPiussi and Sulli, 1995), and under appropriate regional climate conditions, synchronisation between populations can extend over larger spatial scales (Ascoli *et al.*, 2017b). Such synchronisation of cone production can have cascading effects on local communities, starting with the population dynamics of seed predators (Bogdziewicz, Zwolak and Crone, 2016) and extending to pulsed regeneration patterns, interaction with herbivores, and cascading trophic interactions (Ostfeld and Keesing, 2000).

The long-term response of tree reproduction to climate change will be a key factor determining the resilience of forest ecosystems (Caignard *et al.*, 2017; Davi *et al.*, 2016), but the response of masting to ongoing climate change is uncertain (Ascoli *et al.*, 2017b; Pearse, Koenig and Kelly, 2016; Pearse, LaMontagne and Koenig, 2017). Despite their value in addressing how masting will respond to future environmental change, few long-term records of seed production exist, and have revealed contrasting trends. Allen et al. (2014) found a significant increase in seed production in *Nothofagus*, particularly at high elevations, and similar increases in seed production have been reported for other genera (Caignard *et al.*, 2017; Overgaard, Gemmel and Karlsson, 2007). However, in a large study incorporating over 1000 time-series of annual seed production, Pearse *et al.* (2017) found an overall decrease in seed production since 1900. In our study, no significant change in seed production was detected in either a 30-year record of cone production for individual trees, or a stand-level record of seed production that extended over four decades (1971-2012) (Supp. Figure 4). Summer temperatures increased significantly over this period. However, our long-term dataset highlighted the challenges of detecting long-term changes in tree masting. Even with four decades of data, we observed only three large mast events (1976, 1981, 1995), which together accounted for 34% of all seed production despite accounting for only 7% of all monitored years. When such rare events dominate overall seed production, detecting trends in response to climate change is challenging (Vacchiano *et al.*, 2018).

460

461 **4.2 Growth-reproduction relationships: implications for understanding variation in tree growth**

462 The relationship between reproductive effort and tree growth was variable. At the stand scale, mast years
463 were not consistently associated with reduced growth, and we found similar results in a network of Alpine
464 spruce chronologies. At Paneveggio, this generally low sensitivity of growth to investment in reproduction
465 may be related to the generally favourable growing conditions. Paneveggio is a mesic site for spruce, with
466 relatively high annual increment (typically 8-10 m^3 ha^{-1} y^{-1}). Furthermore, the timing of investment in the
467 maturation of cones (including lignification) is likely timed after the main phase of radial growth in early
468 summer (Deslauriers *et al.*, 2008), which may minimise a direct trace-off for resources between radial
469 growth and reproduction. We found evidence that in climatically unfavourable years (cool summers),
470 investment in reproduction was associated with reduced growth; this can be interpreted as a variation in
471 trade-off strength with climate (Hacket-Pain, Lageard and Thomas, 2017; Sletvold and Agren, 2015; Villellas
472 and Garcia, 2018), which can explain the generally weak relationships between growth and masting. We
473 suggest that the population-level insensitivity of growth to masting in warm summers observed at
474 Paneveggio may have resulted from increased resource assimilation during these favourable conditions,
475 reducing any trade-off between competing resource sinks. In an earlier study in the same forests,
476 Mencuccini and Piussi (1995) demonstrated that the negative relationship between growth and seed
477 production was stronger at higher elevations (lower temperatures), supporting our findings for variation
478 between years (Figure 2). Consequently, future environmental changes which favour growth may result in
479 relaxation of growth-reproduction trade-offs in high elevation and temperature limited spruce populations,
480 although this remains to be tested.

481

482 **4.3 Synchronisation of growth within populations: influence of climate and reproduction**

483 Summer (May-July) temperature had a positive influence on radial growth in this population, as has
484 previously been reported from other high elevation spruce stands across the Alps (Castagneri *et al.*, 2014).
485 The response of growth to temperature was generally positive in all individuals, but with weaker

relationships in cone super-producers (Figure 3b). In contrast, the response of growth to reproduction was not consistent between individuals. Variation in trade-off strength between individuals was partly dependent on their long-term cone productivity, such that growth reductions in association with high cone production were generally limited to the heavy cone producers. This is consistent with the findings of Patterson & Knapp (2018) in longleaf pine forests in southeast U.S.A. Consequently, the individualist growth response to individual cone production (Figure 3B), and to population-level mast years (Figure 3C), created increased growth variance in mast years – i.e. less synchronised growth. However, this was not a strong trend, and we did not find consistent results in the regional network of spruce tree ring chronologies.

As heavy cone producers tended to exhibit lower growth in mast years relative to light cone producers, mast years were associated with growth divergences between heavy and light producers (Figure 4). The divergence increased in strength with increased reproductive effort. This result contrasts with Zywiec and Zielonka (2013), who reported no difference in growth between high and low producers in *Sorbus aucuparia* in mast years. However, our results are consistent with numerous reports of growth differences between male and female individuals in dioecious species (Obeso, 2002), where higher reproductive investment by females is associated with lower growth rates than in males. As the individual investment in reproduction was consistent over time (both in absolute cone numbers, and in ranking relative to other individuals), the growth divergence in mast years between heavy and light cone producers was also consistent and extended beyond the period of individual tree cone counts (i.e. 1971-1982, the period with stand-level seed counts only). This indicated that over multiple decades, trees that invested heavily in reproduction showed a reduction in growth relative to trees with low investment in reproduction in mast years. However, BAI 1983-2012 was positively correlated with total cone production over this period (Supp. Figure 6), indicating that long-term high investment in reproduction was not associated with lower growth rates over the study period. If reproductive output is at least partly controlled by genes, it is still unexplained how poor producers are maintained in the population over multiple generations, particularly when our results indicate that high investment in reproduction is not associated with a long-term trade-off with growth. Note that in this study,

512 the 13 trees were growing on a fertile site, on the edge of long-existing canopy gap, and maintained high
513 growth rates over the study period; light cone producers were not suppressed or growing in marginal
514 environments.
515
516 **4.4 Resource switching and implications for understanding masting**
517 At the population level, we found mixed evidence that increased investment in reproduction resulted in a
518 trade-off with growth; some mast years were associated with reduced growth, but not all. In contrast, Selas
519 et al. (2002) reported stronger effects of seed production on growth in spruce (seed production explained
520 42% of variation in ring width), and Mencuccini and Piussi (1995) found a negative relationship between ring
521 width and seed production in spruce stands from our study area. In our study, cone index explained 22% of
522 variation in RWI in years with cool summers, but <2% in analysis including all years, Figure 2B). Other studies
523 have also reported a lack of evidence to support a trade-off between tree growth and reproduction (Zywiec
524 and Zielonka, 2013), including in spruce (Seifert and Mueller-Starck, 2009). Monks and Kelly (2006) argue
525 that evidence of resource switching is the most important evidence that masting results from selection for
526 highly variable seed production, and not simply a response to climate (e.g. resource matching) (see also Kelly
527 and Sork, 2002). Our results imply that resource switching was only required during years of unfavourable
528 resource assimilation, but during more favourable conditions growth rate could be maintained even with the
529 additional demands of developing cones. Furthermore, analysis at the individual level demonstrated that
530 cone super-producers did show a reduction in growth in mast years. Consequently, population-level growth
531 chronologies may mask evidence of switching (Patterson and Knapp, 2018), and where possible, evidence of
532 resource-switching should be sought at the individual level (Monks and Kelly, 2006).
533
534 **4.5 Implications for reconstructing mast years**
535 Multi-decade records of masting are rare (Ascoli *et al.*, 2017a; Kelly and Sork, 2002; PearseLaMontagne and
536 Koenig, 2017), but have revealed important insights into the drivers of changes in masting in response to
537 recent environmental change (Allen *et al.*, 2014; Ascoli *et al.*, 2017b; Pearse, LaMontagne and Koenig, 2017).

Where such long observational records do not exist, reconstructions of mast years using tree ring chronologies may facilitate improved understanding of the response of masting to long-term environmental change, and cascading impacts of these changes on forest ecosystems more generally (Ostfeld and Keesing, 2000). For example, Drobyshev (2014) used a multi-century reconstruction of beech mast events in Sweden to demonstrate that decadal changes in mast frequency were not linked to changes in nitrogen deposition (as proposed by Overgaard et al. 2007). However, our results indicate that not all mast years are associated with a reduction in growth (Figure 2), with significant growth reductions limited to years with unfavourable climate (see Hacket-Pain *et al*. 2017 for similar findings for *Fagus sylvatica*). In this case, negative pointer years in ring width series may not be enough to identify all mast years, even if combined with historical climate data for the known climate cues of mast years (the method of Drobyshev *et al.* 2014). A more complete integration of climate data and tree rings may be required, accounting for factors that influence the sensitivity of ring width to masting events, but mast years that coincided with climatically favourable years may ultimately be harder to detect. However, other tree ring parameters may also provide information on masting. For example, Han *et al.* (2016) reported small differences in $\delta^{13}C$ in tree rings associated with mast years in *Fagus crenata*, and Rodríguez-Ramírez *et al.* (2018) showed potential for mast year reconstruction based on wood anatomical traits. Additionally, our results indicate that the individualist responses of trees to masting may also prove useful in identifying mast years using individual tree ring data. For example, increased between-tree growth variability may be useful for identifying mast years, and requires no additional information on the sampled trees. This may be a useful source of information to identify mast years (particularly heavy mast years) (Figure 4), and contribute to a “toolbox” of useful indicators for tree-ring based reconstruction of mast years.

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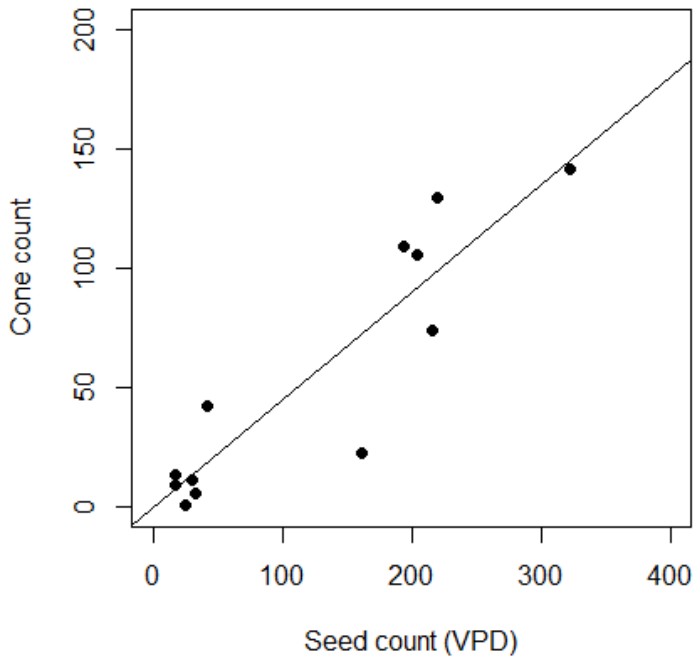
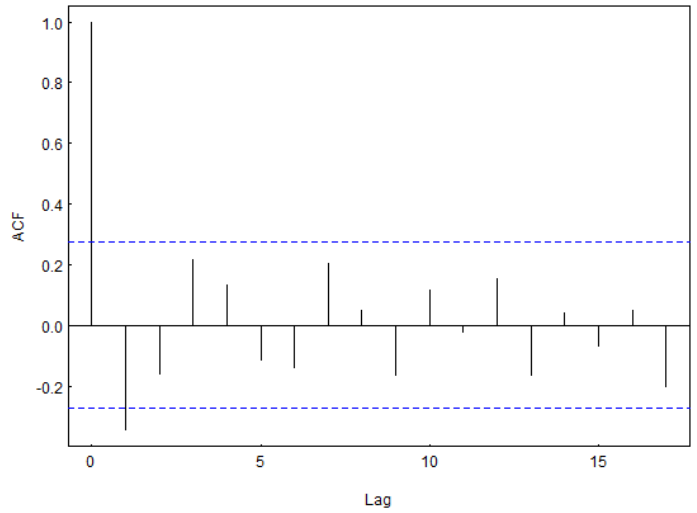
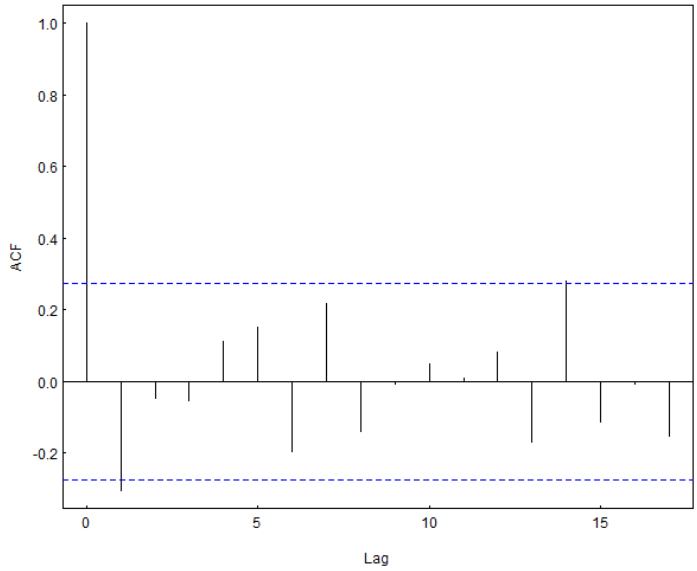
Supplementary Figures

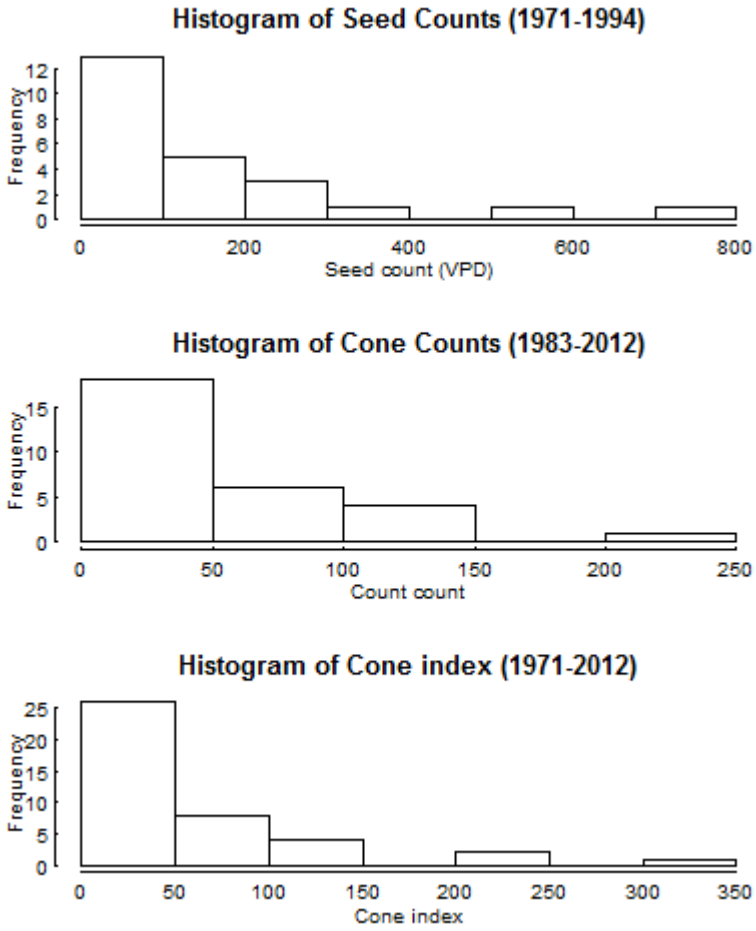


Supp. Figure 1. Relationship between mean stand cone counts and mean seed count for Paneveggio (VPD, sum of viable, predated, damaged seeds), 1983-1994. $R^2 = 0.82$, $p<0.001$.





Supp. Figure 2. Autocorrelation functions for cone production (1982-2012) (top panel) and cone index (1971-2012) (bottom panel)



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580 **Supp. Figure 3.** Distributions of measures of seed and cone production

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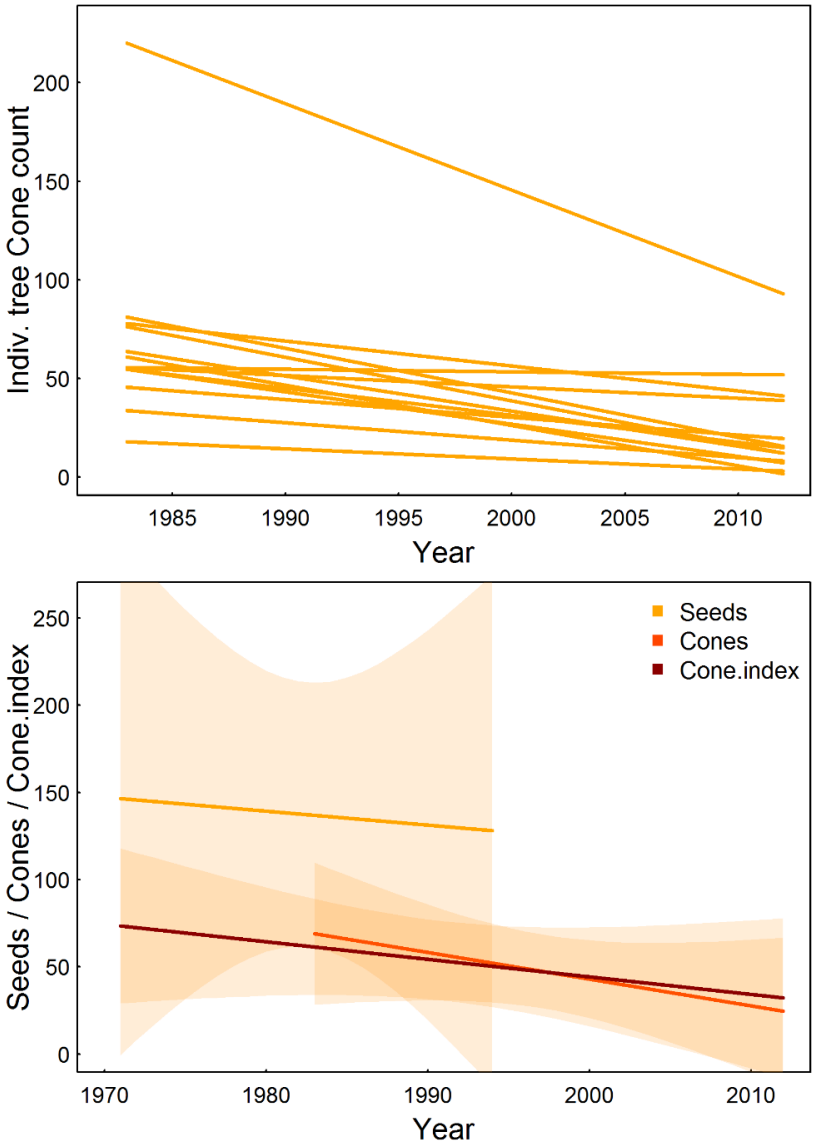

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584 **Supp. Figure 4.** Linear trends in cone counts for 13 individual trees. All trends were insignificant at 95%

585 confidence level (top panel). Linear trends in stand-level measures of seed/cone production. All trends were

586 insignificant at 95% confidence level (bottom panel).

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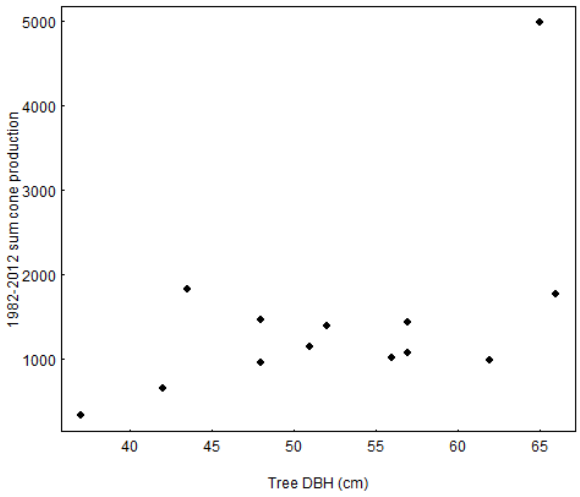
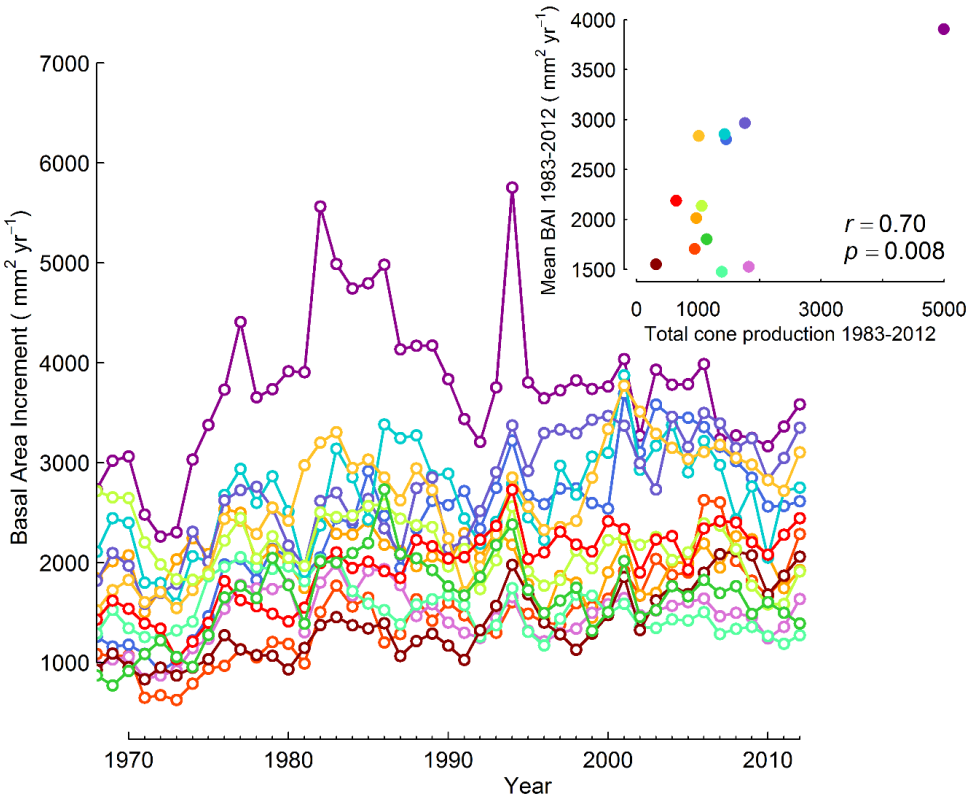
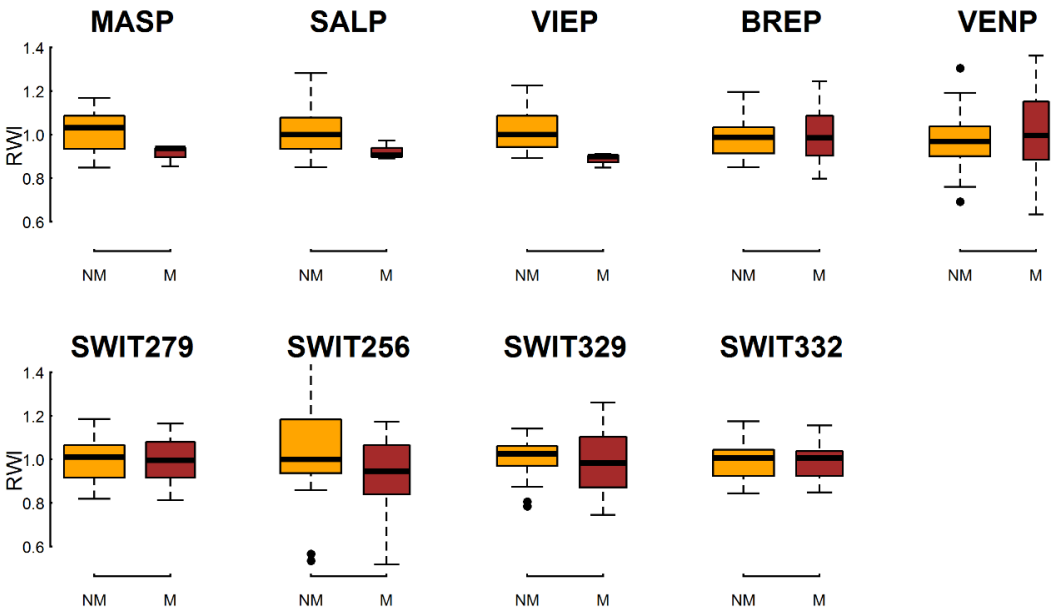


Supp. Figure 5. Relationship between tree diameter at breast height (DBH) and total cone production (1983-2012)

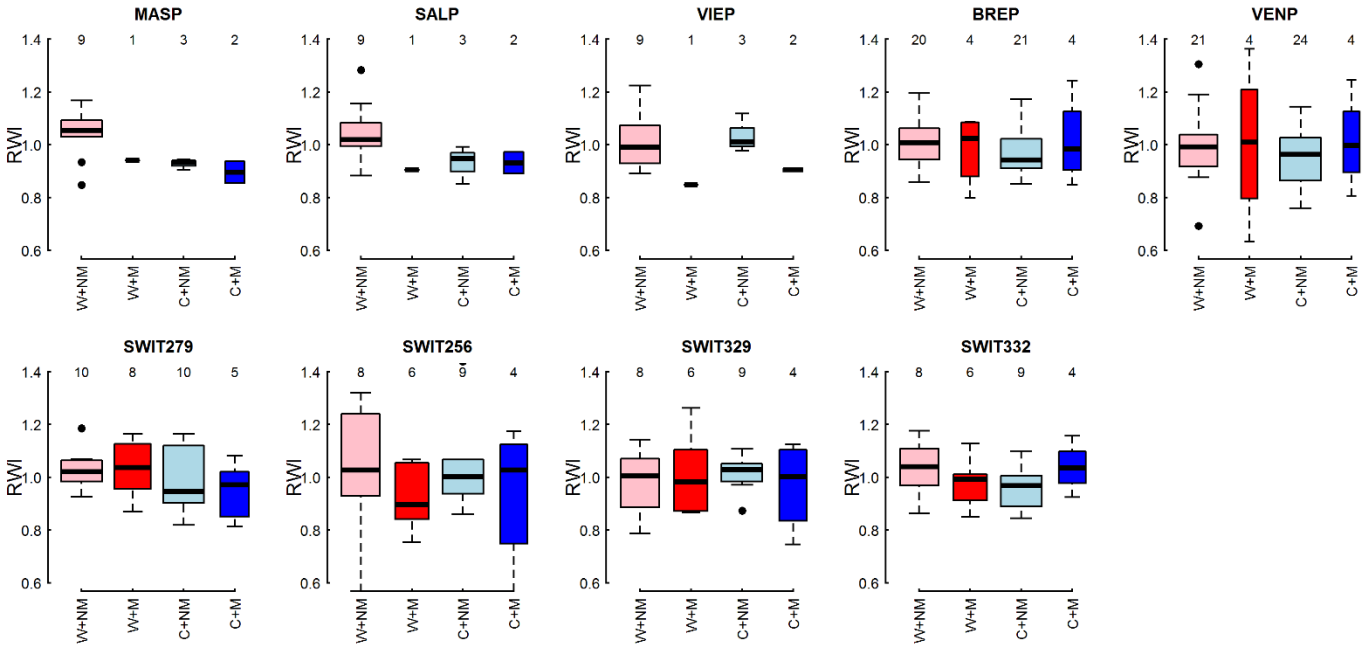


Supp. Figure 6. Basal Area Increment (BAI) chronologies for each individual. Line colour represents the individual tree ranking for total 1983-2012 cone count; heavy cone producers are purple/blue, and light producers are orange/red. Inset plot shows the relationship between total cone production (1983-2012) and individual tree BAI over the same time period.

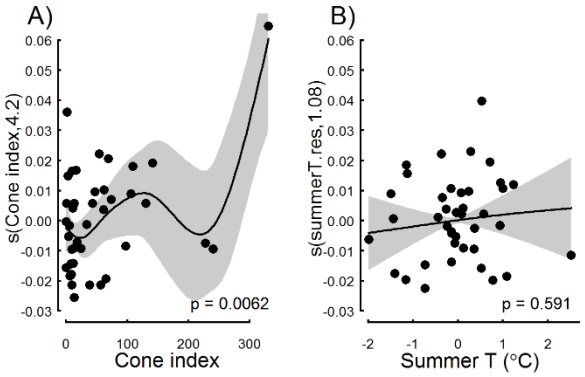


Supp. Figure 7. Boxplots of RWI according to regional masting category (mast years taken from the MASTREE database for ITC, ITH and CH0). Orange = non-mast year, brown = mast year.

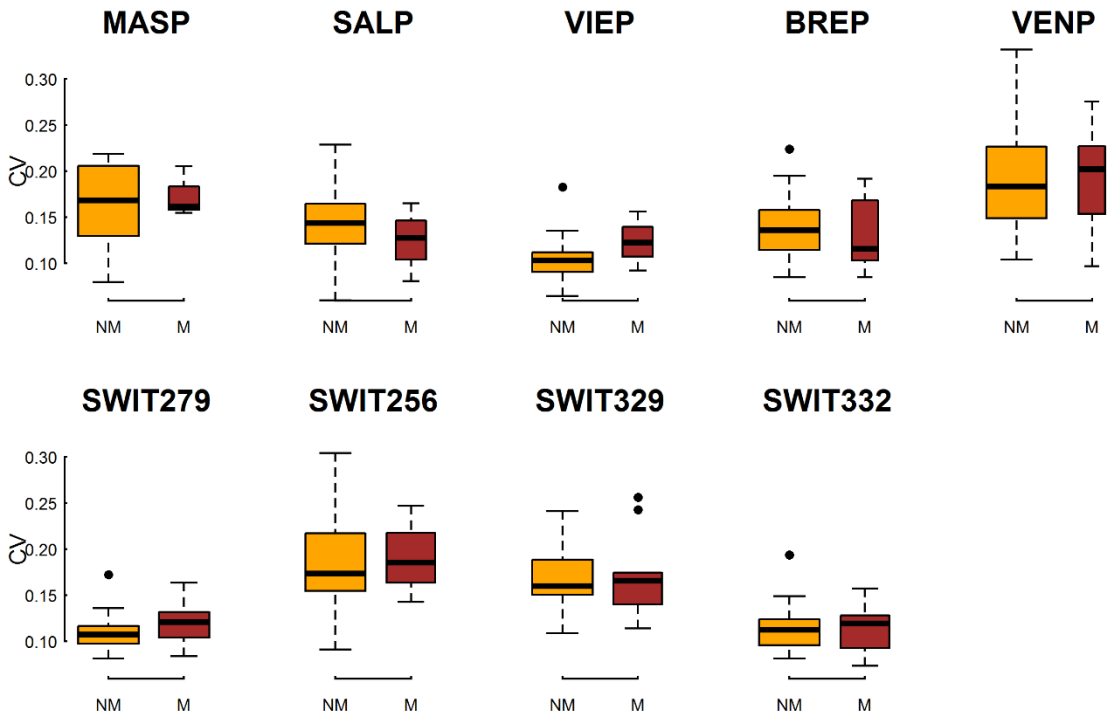
Difference in RWI between NM and M years marginally significant for VIEP (p=0.0484, Wilcoxon test)



Sup. Figure 8. Boxplots of RWI according to summer temperature and masting. Red = warm summers (W), Blue = cool summer (C). Pale = non-mast (NM), bright = mast (M) year.



Supp. Figure 9. GAM models with 95% confidence intervals for between-tree growth CV and A) cone index, B) summer temperature. The smoother for Cone Index is significant, showing an increase in growth CV (a decline in synchrony) in years of high seed production at the stand level, but not significant relationship with summer temperature (May-July).



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621 **Supp. Figure 10.** Boxplots of CV_{RWI} according to masting status in Alpine spruce tree ring chronologies. No

622 differences were statistically significant (Wilcoxon tests). Orange = non-mast year, brown = mast year

623

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